

How Navigational Guidance Systems Are Combined in a Desert Ant

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Summary

Animals use information from multiple sources in order to navigate between goals [1]. Ants such as *Cataglyphis fortis* use an odometer and a sun-based compass to provide input for path integration (PI) [2]. They also use configurations of visual features to learn both goal locations [3–5] and habitual routes to the goals [6–10]. Information is not combined into a unified representation [11–14] but appears to be exploited by separate expert guidance systems [10, 15, 16]. Visual and PI goal memories are acquired rapidly and provide the consistency for route memories to be formed [17, 18]. Do established route memories then suppress the guidance from PI? A series of manipulations putting PI and route memories into varying levels of conflict found that ants follow compromise trajectories. The guidance systems are therefore active together and share the control of behavior. Route memories do not suppress the other guidance systems. A simple model shows that observed patterns of control could arise from a superposition of the output commands from the guidance systems, potentially approximating Bayesian inference [19]. These results help show how an insect's relatively simple decision-making can produce navigation that is reliable and efficient and that also adapts to changing demands.

Results and Discussion

Cataglyphis fortis forages individually over large distances using spatial memories rather than pheromone trails [20]. Path integration (PI) provides a forager with a record of its cumulative travel from the nest—its nest-based PI “coordinates.” To use this information to determine a heading direction, a forager essentially subtracts its current PI coordinates from the remembered PI coordinates of that goal [21]. Because the information is derived from ideothetic cues, the resultant “PI output vector” [14] can guide travel across even unfamiliar areas and can compensate for detours [21, 22].

When an ant follows a path repeatedly, it learns the heading directions along the path [10, 11, 23]. These habitual heading directions appear to be encoded in terms of the visual panorama [7, 9, 24, 25]. Along a route, an ant rotates so that its current view aligns with the best-matching “snapshot” memory [10, 25, 26]—“alignment image-matching.” The habitual heading directions, sometimes known as “local vectors” [11], may also be associated with the distance over which the heading direction is followed [14, 27, 28]. A visual route, likely composed of a sequence of such heading directions [10, 24, 29], can be followed whether or not information is available from PI [30, 31].

The question asked here is whether, after extensive experience along a route, travel is guided solely by habitual route

memories or whether the PI output vector also remains involved. In other words, do the procedural local vector route memories, for which headings may simply be recalled, suppress the use of the goal-based PI memories, which require the heading directions to be computed each time?

Manipulating the Path Integration Output Vector

Ants were trained to follow a two-leg route (Figure 1A) along which it was possible to manipulate cues from PI in order to put PI-based guidance into varying levels of conflict with visual-based memories at a distinctive decision point (Figure 1B). The first leg from the nest was through a 10 m long channel that was open-topped so that ants could obtain the sky-compass cues required for PI. An exit ramp at the end lead to a particularly bare and uniform area of open ground from where the distant surrounding panorama was visible in all directions and ants could choose their paths freely (Figure 1C). A feeder was located 6 m perpendicular to the channel. To test the generality of the results, three different configurations of artificial landmarks were placed near the route: a relatively landmark-rich “configuration A” ranging to a landmark-poor “configuration C” (see Figure S1 available online).

Studies suggest that the ant's PI system does not have access to information from visual features. If an experimenter displaces an ant to a familiar location along its route, then the ant's PI coordinates will reflect the cumulative distance it has walked from the nest, and not the location it is displaced to [11, 12, 14, 30, 32]. In other words, although a familiar view may trigger a habitual route memory, it does not cause an ant to adjust its PI coordinates. It was therefore possible to manipulate the PI coordinates with which ants emerged onto the open ground. During a test, ants were transported from the nest area to partway along the channel before being released to travel the remaining distance. In this way, conflicts were induced between the computed PI output vector and any habitual route memories (Figure 1B). If ants rely solely on the route memories, then such manipulations should have no effect on the trajectories from the channel.

To analyze the effects of the experimental manipulations, “reference” trajectories of individually marked ants were first recorded as the ants traveled to the feeder normally (Figure 1Di). The next time one of those individuals was observed leaving the nest, it was transported 4 m along the channel. When the ant emerged onto open ground, having then run only the last 6 m of the channel, its “test” trajectory was recorded (Figure 1Dii). These trajectories have an initial straight segment 4–6 m long often ending in a curve toward the feeder. For training with the landmark rich configuration A, there is a strong correlation between the initial directions (calculated throughout as the resultant over the first 3 m) of an ant's reference and test trajectories (Figure 1E, $p < 0.01$; $\text{Rho} = 0.67$, $n = 21$). Thus, even over this single open segment, the ants have consistent individual idiosyncrasies indicative of habitual route memories [31]. Results are more complicated, but potentially consistent, for training with the landmark-poor configuration C (see Figure S1).

Individual idiosyncrasies can be filtered out from the analysis by using “residual” directions—calculated as the direction of an ant's test trajectory minus the direction of its

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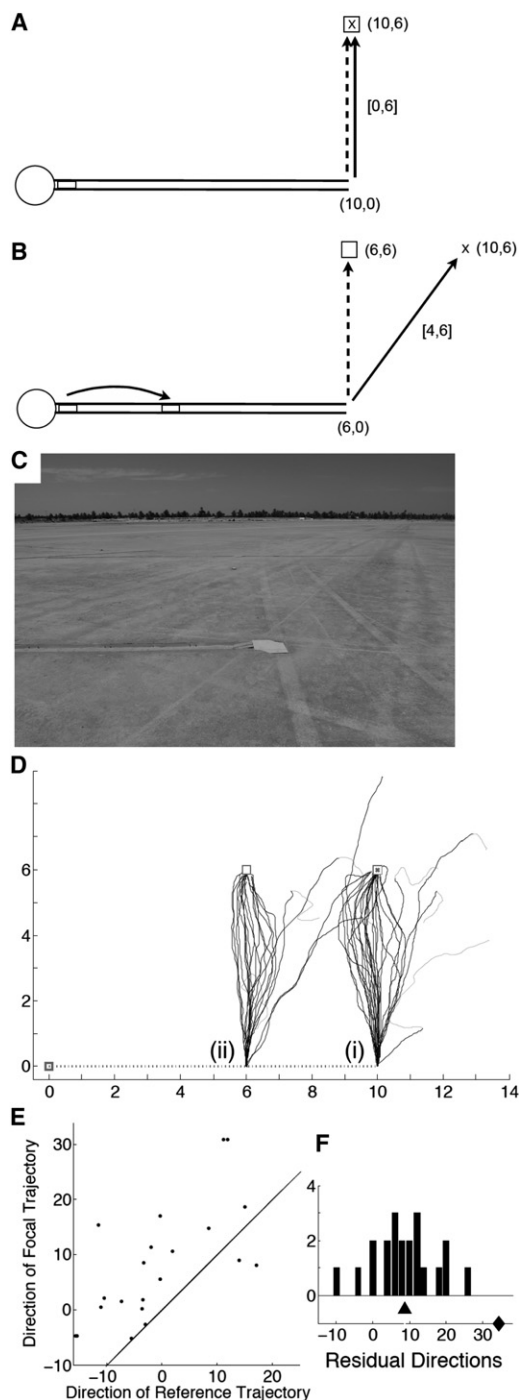


Figure 1. Manipulating PI along a Habitual Route

(A) Schematic of the training route. An enclosure (circle) surrounded the nest, opening into a moveable tray (rectangle) that sat in the channel (parallel lines). The feeder (square) lay 6 m from the ramp at the end of the channel. The dashed arrow represents the local vector route memory. The PI output vector calculated at the end of the channel is represented by the solid arrow and by the coordinates in square brackets. The coordinates in curved brackets indicate an ant's global PI coordinates at significant positions. The PI-based goal is indicated by the cross (in this condition it coincides with the feeder).

(B) Schematic of the PI manipulation on the training route. An ant is carried 4 m in the tray (curved arrow) before being released to run along the channel. The ant's global PI coordinates and the position of its PI-based goal (cross) are thus shifted 4 m with respect to training. The local vector (dashed arrow) and PI output vector (solid arrow) therefore no longer coincide.

reference trajectory. These residual directions (Figure 1F) are small ($7.6 \pm 9.6^\circ$, $n = 21$), but consistently (19/21) and significantly ($p < 0.01$, M test) greater than zero. They reflect 26% of the difference between the reference trajectories and the predicted PI output vector (suggesting that the PI output vector provides at least 26% of the input to the heading direction. See Figure 4E for why the contribution from PI is probably greater).

Compromise between Local Vectors and PI Guidance

Further evidence that the PI output vector contributes to guidance alongside the local vectors is provided by a series of manipulations carried out at a parallel test channel (Figure S1) from which the distant panorama was essentially the same but the artificial landmarks and any potentially familiar surface features would be absent. During each manipulation, ants were transported to a specific position in the test channel so that they walked 2 m, 6 m, 10 m, or 14 m before reaching the exit ramp. The distance walked had an obvious effect on the directions taken (Figures 2A and 2B), confirming that the trajectories result from compromises between the local and PI output vectors. The shorter the distance, the greater the residuals between test and reference trajectories (Watson-Williams between residuals. 2 m versus 6 m: $p = 0.051$, $F = 4.2$; 6 m versus 10 m: $p = 0.067$, $F = 3.7$; 10 m versus 14 m: $p = 0.11$, $F = 2.7$. For 2 m versus 10 m and 14 m, and 6 m versus 14 m, $p < 0.0001$. Training with configuration B). When test channel lengths are shorter than training, the residuals are approximately half of the difference between the predicted PI output vector and the mean reference directions (2 m, 48%; 6 m, 44%). These results are consistent across training configurations (6 m with configuration A, 44%; 6 m with configuration C, 57%; see Figure S2). If local vectors are aligned with the reference directions, this result suggests that (in this condition) the local and PI output vectors provide approximately equal input to the heading direction.

An additional manipulation at the test channel suggests that interactions between local vectors and PI output vectors may affect the lengths, as well as the directions, of the straight segments. Ants were tested from an oblique test channel that corresponded approximately to the direct path between the nest and feeder (Figure 2C). On emerging from this channel, an ant's current PI coordinates would have been close to the remembered coordinates of the feeder, and so the computed PI output vector should be extremely short.

(C) Photo of experimental area. The channel and feeder were dug into the ground to make them inconspicuous. The wheel tracks, although striking from above, were not followed by the ants. Note the distant trees that are visible on the landward side of the panorama. More photos in Figure S1.

(D) Trajectories along the habitual route from the training channel. (i) Reference trajectories. (ii) Test trajectories after PI manipulation. The coordinate system reflects an ant's PI global coordinates (in meters). Thus for the test trajectories, the feeder is at (6,6), indicated by the square, although the PI output vector is directed toward (10,6), indicated by the cross. Final convergence to the feeder (squares) can be guided by visual, and in some cases odor (see Figure S1), cues.

(E) Relationship between the initial directions (over first 3 m) of an ant's reference trajectory ($-0.7 \pm 9.8^\circ$) and its test trajectory ($8.1 \pm 10.2^\circ$). Throughout, data are given as mean \pm SD. Angles are measured clockwise from the direct path. Each point is a single ant ($n = 21$). The diagonal line indicates where the two would be equal.

(F) Histogram of the residual directions (corresponds to vertical distance from diagonal line of points in E). The triangle beneath the scale shows the mean, and the diamond indicates the PI-based prediction—an accurate PI output vector minus the mean reference direction. See also Figure S1.

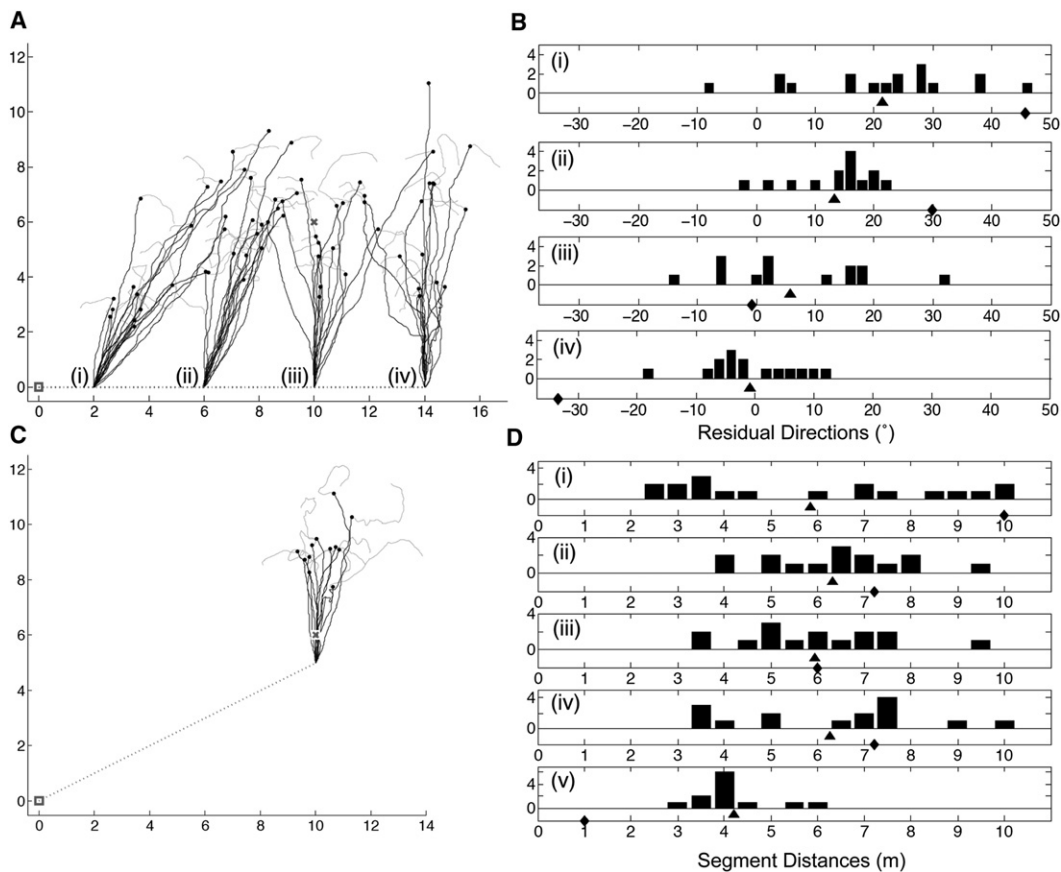


Figure 2. Manipulations of PI State on Test Ground

(A) Trajectories from the test channel. Training is with configuration B (see Figure S1). Coordinates reflect the ants' global PI coordinates. The *abknicht* on each trajectory is indicated by a point, and the beginning of the subsequent search is shown in light gray. (i) 2 m manipulation; (ii) 6 m manipulation; (iii) 10 m manipulation; (iv) 14 m manipulation.

(B) Histograms of residual directions between test and reference trajectories in (A). (i) 2 m manipulation. Residual directions = $22 \pm 14.3^\circ$ (mean \pm SD), $n = 17$. (ii) 6 m manipulation. Residual directions = $13.2 \pm 6.7^\circ$, $n = 14$; (iii) 10 m manipulation. Residual directions = $5.7 \pm 12.4^\circ$, $n = 14$; (iv) 14 m manipulation. Residual directions = $-0.8 \pm 7.8^\circ$, $n = 14$.

(C) Manipulation with an oblique channel during training with Landmark configuration A. Residual directions = $4.0 \pm 7.1^\circ$. Note that the trajectories do not rotate with the direction of the preceding channel.

(D) Histogram of lengths of trajectories before *abknicht*. (i) 2 m manipulation. Lengths = 5.8 ± 2.9 m, $n = 18$; (ii) 6 m manipulation. Lengths = 6.3 ± 1.5 m, $n = 15$; (iii) 10 m manipulation. Lengths = 5.9 ± 1.7 m, $n = 15$; (iv) 14 m manipulation. Lengths = 6.3 ± 2.2 m, $n = 15$; (v) Oblique manipulation. Lengths = 3.9 ± 0.7 m, $n = 12$. See also Figure S2.

The lengths of the test trajectories in this condition are intermediate between those from the other conditions and the 1 m length expected from a PI output vector (Figure 2D). There is no obvious correlation between the sizes of residuals and lengths of initial segments (2 m, 6 m, and 10 m tests combined: $p > 0.2$, $Rho = 0.196$, $n = 45$), suggesting that the distance and the direction interactions may be separate processes.

The compromises observed here suggest a reinterpretation of previous results. In one study, rotating a large portion of the visual panorama provided clear evidence for view-based route memories and, when a PI output vector was available, for a compromise between those route memories and some form of compass-based guidance [7]. At the time, it was believed that local vectors were a distinct, compass-based, route memory, and that the observed compromise was between those two putative forms of route memory. However, there is no strong evidence for compass-based route memories (putative examples at coastal sites here and elsewhere [4, 7, 10, 11, 18] may instead be using differences in distant

skyline or UV contrast between landward and seaward sides). The observed compromise was probably, as is shown unambiguously in the present study, between route memories and a PI output vector. Similarly, compromises observed when honeybees were trained to one route and then exposed to waggle dances indicating a different direction [33], could also be a compromise between a local vector memory and a PI-based heading direction.

Navigational Control from the Superposition of Guidance Commands

There are several ways that information from multiple sources can be integrated to control behavior. Previous studies suggest that navigational information in *C. fortis* is not combined into a unified spatial representation but is instead processed by separate, potentially modular, guidance systems [11, 13, 14, 30]. If so, then the convergence must occur at the level of their computational outputs. A compromise heading could then be produced in a common encoding where those

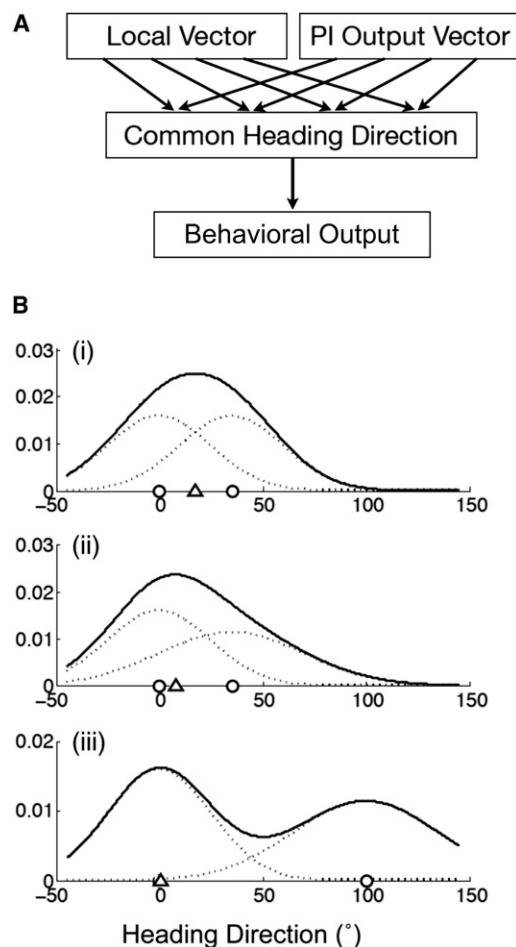


Figure 3. Convergence of Independent Navigational Guidance Systems into a Common Population Encoding of Heading Direction

(A) Schematic of navigational architecture showing the processing stage at which information may be combined.

(B) Activation patterns in a common population encoding. The resultant (solid line with peak indicated by a triangle) arises from a simple superposition of the heading directions from two guidance systems (dashed lines with peaks indicated by open circles). (i) The compromise is biased when two activation patterns have equal variance. (ii) The compromise is biased when two activation patterns have unequal variance. (iii) There are multiple peaks when activation patterns are widely divergent.

outputs converge (Figure 3). The idea that outputs from the navigational systems converge onto a common encoding of heading direction has also been proposed in a recent model [15] that also appears to be based largely on the work cited here (particularly [11, 12, 14, 21]). The compromise trajectories described here, however, suggest a simpler way in which the output commands may be integrated: as a superposition in a population encoding.

If the outputs from two guidance systems produce overlapping activation patterns, then these patterns may combine to produce an intermediate peak (Figure 3Bi). The intermediate peak would then produce a trajectory that reflects a compromise between the guidance systems. Compromises, however, need not reflect the guidance systems equally. A guidance system that produces a weak or diffuse activation pattern will have less influence on the position of a resultant peak than does a system that produces a sharper activation pattern (Figure 3Bii). Navigational systems would thus automatically have

greater influence when they produce a more precise guidance command. Finally, if differences between the guidance systems are large, then the resultant activation pattern will have multiple peaks (Figure 3Biii). This can explain why ants are able to recapitulate habitual routes, even when a PI output vector points diametrically opposite [23, 30]. With this model, transitions in the balance of navigational control need not require any top-down or contextual modulation of weightings, nor any interactions between systems outside of the common encoding (for instance modulations of salience *sensu* [15]).

The patterns of interactions shown in the ants' navigation, and in the superposition model (Figure 3), resemble the optimal outcomes described by Bayesian decision-making. Whether the resemblance is more than superficial is unclear, but the superposition of individual directional preferences into a population coding, such as that proposed here, can theoretically produce Bayesian outcomes [19].

Contributions from Goal-Directed Image-Matching?

PI and the distant panorama are not the only factors guiding the ants to the feeder. Nearby landmarks also play a role and are responsible for at least one very obvious difference between the trajectories from the training and test channels. Trajectories from the training channel generally converge toward the feeder (Figure 1), whereas at the test area they end in search (Figure 2). By removing all nearby landmarks, convergence on the training route can also be abolished (Figures 4A–4C; Figure S3) [18, 21].

The convergence is thought to result from a mechanism of “goal-directed image-matching” (GDIM). On the first few departures from its nest or a food-site, an ant (like other hymenoptera e.g., [34–36]) performs a stereotyped behavior that appears adapted to learning some kind of snapshots of the constellation of surrounding features [37, 38]. In subsequent approaches, it uses disparities between its current view and those remembered goal snapshots to head toward the encoded location [5, 39]. Unlike the alignment image-matching used to recover habitual (local vector) heading directions, GDIM dominates when an ant is away from, or toward the end of, its route [10, 26].

In addition to their obvious influence near the goal, the nearby landmarks also affect the initial directions of the trajectories. Previous studies suggest that there is a systematic under-turn when guidance by PI produces a sharp change in direction [21], and that the under-turn is reduced by the presence of nearby landmarks [18]. This under-turn is unmasked here when the landmarks are removed (Figures 4A–4D).

Both effects, and the learning of routes more generally, can be explained by additional input from GDIM into the common encoding. With landmarks present, GDIM could provide a precise guidance cue as soon as an ant emerges from the channel (Figure 4Ei). But without nearby landmarks, the panoramic view included only the more distant skyline and thus varied little over the open area from the channel. GDIM would then direct ants to anywhere within a relatively wide area around the feeder, producing a broad activation pattern that would not counteract the under-turning (Figure 4Eii). During extended training without landmarks, the local vector would gradually shift to reflect the new balance between GDIM and PI (Figure 4Eiii).

Conclusions

PI-based guidance and goal-directed image-matching using snapshots from near the goal can be used on the very first

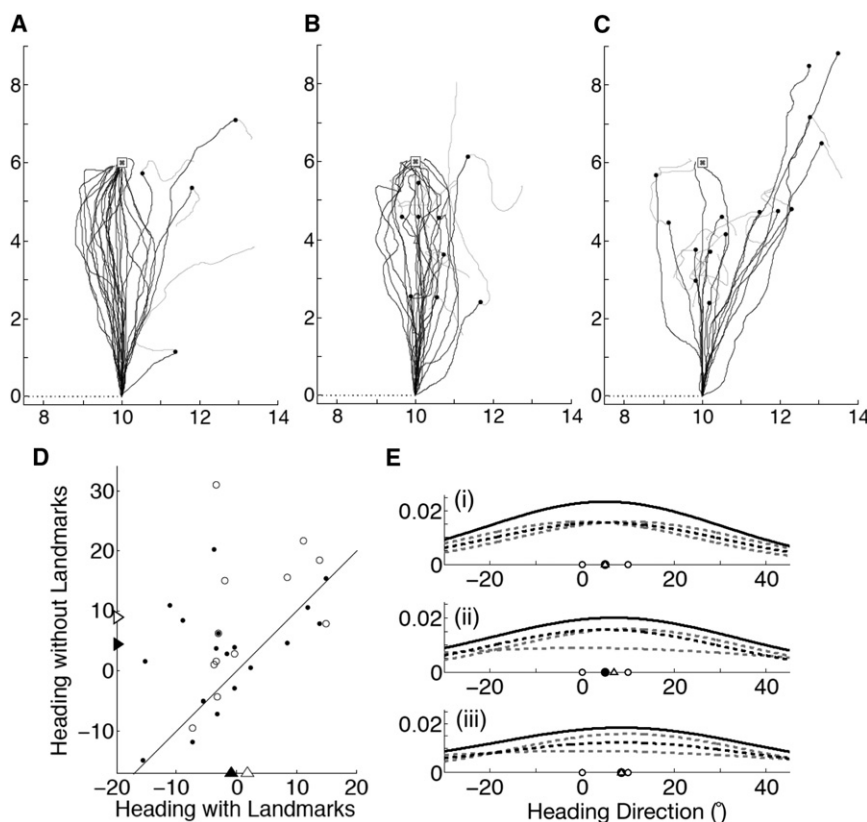


Figure 4. Influence of Landmarks on Habitual Route

During training, landmarks were in configuration A. (A) Reference trajectories; $n = 27$. Abknichts are shown in the four trajectories that do not reach the feeder directly (15%).

(B) Feeder-landmark removed. Note that the convergence is not simply beaconing, because removing the feeder-landmark alone does not abolish the convergence; $n = 23$. Abknichts shown in nine trajectories (39%).

(C) All three artificial landmarks removed; $n = 17$. Abknichts shown in 15 trajectories (88%).

(D) Correlations between reference and test trajectories when only the feeder landmark is removed (filled circles, $n = 20$. Residual directions = $5.0 \pm 9.2^\circ$) and when all three artificial landmarks are removed (open circles, $n = 12$. Residual directions = $7.3 \pm 10.0^\circ$). Means of reference and test trajectories shown as triangles (filled and open) on the axes.

(E) Superposition of three guidance systems. Further details of the model are in [Supplemental Experimental Procedures](#). (i) Training with a rich landmark configuration. GDIM is centered at 0° with $SD = 25^\circ$. The PI output vector is centered at 10° (reflecting systematic under-turning) with $SD = 25^\circ$. Both patterns are shown as pale dashed lines with peak directions indicated by pale circles. The local vector (dark dashed line) is derived from the superposition of GDIM and the PI output vector. Peak direction (dark circle) lies under the peak direction of resultant (triangle). (ii) Superposition when artificial landmarks are removed. GDIM is given $SD = 45^\circ$ but all other parameter remain constant. (iii) Extended training with landmarks removed. The local vector reflects the superposition of the PI output vector and new GDIM. See also [Figure S3](#).

return trips to a location. These primary guidance systems provide a consistent scaffolding that allows habitual route memories to develop [17, 18]. Route memories then produce paths that are more precise [27], and they can be used even in the absence of a celestial compass [40]. The results here show that, whereas route memories may become increasingly important, the scaffolding provided by the primary goal-directed systems remains in place and continues to contribute to guidance. In most natural routes, PI-based guidance and GDIM will continuously pull routes (near the beginnings and ends, respectively) toward the direct efficient line. If an individual starts to exploit a new food location, then PI and GDIM immediately pulls the path toward the new line. Over repeated trips there may also be a more gradual shift as local vector route memories again become aligned with the balance between the other guidance systems [18]. The multiple systems thus combine to produce routes that are efficient and that can also adapt to changes in the location of a goal or in the obstacles along the way.

Compromises between directional cues may well prove a general phenomenon in insect guidance [6, 7, 33, 41–44]. The simultaneous use of multiple systems described here suggests that the ant's navigation is not organized as a hierarchy of systems and that there need not be some form of top-down or executive control that gates the different guidance systems. Instead, the interactions can be thought of as a type of collective decision-making, analogous to those within groups of animals [45]. The coordinated behavior can arise, without any form of centralized control, from the

interactions between individual units that may each have a directional preference developed from its own individual information processing. The superposition model of navigational control (Figure 3) shows how ants may integrate their multiple sources of information, possibly approximating a Bayesian optimum [19], to produce navigation that is both reliable and flexible, even without the cognitive complexity that is available to large-brained mammals.

Supplemental Information

Supplemental Information includes three figures and Supplemental Experimental Procedures and can be found with this article online at [doi:10.1016/j.cub.2012.03.049](https://doi.org/10.1016/j.cub.2012.03.049).

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